AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3447, 12 pp., 3 figures, 2 tables June 2, 2004

New Avialan Remains and a Review of the Known Avifauna from the Late Cretaceous Nemegt Formation of Mongolia

JULIA A. CLARKE[1] AND MARK A. NORELL[2]

ABSTRACT

Small vertebrates have remained relatively poorly known from the Nemegt Formation, although it has produced abundant and well-preserved large dinosaur remains. Here we report three new avialan specimens from the Late Cretaceous (Maastrichtian) of Omnogov Aimag, Mongolia. These fossils were collected from the Nemegt Formation exposed at the locality of Tsaagan Khushu in the southern Gobi Desert. All of the new finds are partial isolated bones with a limited number of preserved morphologies; however, they further understanding of dinosaur diversity in the Late Cretaceous of Mongolia and, specifically, from the Nemegt Formation. The new specimens are described and evaluated in phylogenetic analyses. These analyses indicate that all three fossils are placed as part of the clade Ornithurae.

Avialan diversity of the Nemegt Formation is reviewed and briefly compared with that of the underlying Djadokhta and Barun Goyot Formations. These formations have been considered to represent at least two distinct Late Cretaceous environments, with the Nemegt typically interpreted as representing more humid conditions. Ornithurine and enantiornithine birds are known from the Nemegt as well as the Djadokhta and Barun Goyot Formations, although ornithurine remains are more common in the Nemegt. No avialan species known from the Djadokhta, or Barun Goyot, are also known from the Nemegt Formation and, overall, the avialan taxa from these formations do not appear more closely related to each other than to other avialans. Whether these faunal differences are best interpreted as environmental, temporal, or sampling/preservational should be further investigated.

[1] Division of Paleontology, American Museum of Natural History; North Carolina State University and North Carolina Museum of Natural Sciences (Julia_Clarke@ncsu.edu).
[2] Division of Paleontology, American Museum of Natural History (norell@amnh.org).

Copyright © American Museum of Natural History 2004 ISSN 0003-0082

SHOUT
SHARE
IT

Fig. 1. Map of Mongolia indicating where the fossils were recovered, the locality of Tsaagan Khushu in the western Gobi Desert (Omongov Aimag).

INTRODUCTION

Three new avialan fossils were collected from the Maastrichtian (Martinson et al., 1969) Nemegt Formation (Efremov, 1954; but see Gradzinski et al., 1977) in southern Mongolia by the Mongolian Academy of Sciences/American Museum of Natural History (MAS/AMNH) expeditions in 2000 and 2001. The finds are all partial, isolated bones recovered from the western exposures of Tsaagan Khushu (Gradzinski et al., 1977), a locality in the Nemegt Basin (Omongov Aimag, Mongolia; fig. 1). All three specimens were found in distinct, small, well-sorted sand lenses comparatively rich in isolated small vertebrate elements (e.g., fish vertebrae, turtle plastron, and carapace fragments). A proximal tibiotarsus (IGM 100/1311) described here was discovered during the 2000 MAS/AMNH expedition, and a distal tibiotarsus (IGM 100/1310) as well as a proximal humerus (IGM 100/1309) were collected in 2001. None of the specimens appears to be from a juvenile animal; muscular scars and tubercles are well developed, the bone surfaces are smooth, and the proximal tarsals are completely fused to the tibia in IGM 100/1310.

The Nemegt Formation has been interpreted as representing a dominantly fluvial environment with most fossils from channel fill, point bar, and occasional overbank deposits laid down under more humid conditions than in the underlying Djadokhta Formation (Gradzinski, 1970; Jerzykiewicz and Russell, 1991). In marked contrast to the underlying Djadokhta Formation (Dashzeveg et al., 1995), the remains of small vertebrates are rare from the Nemegt Formation, which has produced abundant and well-preserved large dinosaur remains (Osmólska, 1980; Barsbold, 1983). The Nemegt fauna has also been described as more cosmopolitan than that of the Djadokhta, having stronger affin-

ities to faunas from North American Late Cretaceous localities (Jerzykiewicz and Russell, 1991).

Previously described avialan remains from the Nemegt Formation include five isolated and incomplete bones referred to the Hesperornithes (Kurochkin, 2000) and two specimens comprising associated forelimb elements that are the holotypes of the enantiornithine *Gurilynia nessovi* (Kurochkin, 1999) and proposed presbyornithid anseriform *Teviornis gobiensis* (Kurochkin et al., 2002). The small theropod *Mononykus olecranus* (Perle et al., 1993) was also described from the Nemegt Formation (at Bugin Tsav) as a basal avialan (Perle et al., 1993); however, this taxon and other alvarezsaurids are now most often placed phylogenetically outside Avialae (e.g., Norell et al., 2001). The existence of specimens of "graculavid charadriiforms" or "transitional shorebirds", and crown clade avian taxa including presbyornithid anseriforms, phalacrocoracids, and diomediids, in the Nemegt Formation has also been indicated (Kurochkin, 2000: 556). However, so far only one of these specimens has been described (Kurochkin et al., 2002) and one isolated tarsometatarsus from the Barun Goyot Formation (Kurochkin, 2000) was recently removed from the Presbyornithidae (Kurochkin et al., 2002). Thus, with the exception of the large enantiornithine *Gurilynia nessovi*, all of the avialan taxa from the Nemegt have been considered parts of Ornithurae, either as relatively closely related to Aves as part of Hesperornithes, or as parts of crown clade avian lineages.

The taxonomic status of previously discovered avialan fossils from the Nemegt Formation is briefly reviewed here, and known Nemegt avialan diversity is compared to that from the underlying Djadokhta and Barun Goyot Formations. Gradzinski et al. (1977) suggested, on the basis of faunal differences, that the Barun Goyot Formation was younger than the Djadokhta Formation. However, more recent work has not supported this conclusion, instead implying that the Djadokhta and Barun Goyot are nearly coeval (Jerzykiewicz and Russell, 1991; Dashzeveg et al., 1995; Jerzykiewicz et al., 1993; Gao and Norell, 2000).

INSTITUTIONAL ABBREVIATIONS: **AMNH,** American Museum of Natural History; **IGM,** Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar.

DESCRIPTION OF THE NEW MATERIAL

IGM 100/1309 is a proximal left humerus (fig. 2A; table 1). The humeral head is globose but comparatively weakly expanded proximally and anteroposteriorly. The pneumotricipital fossa is comparatively diminutive, does not excavate the distal surface of the ventral tubercle, and does not contain any pneumatic foramina. The dorsal surface of the ventral tubercle bears a depressed, subtriangular scar. The bar that demarcates the dorsal edge of this fossa in Aves (crus dorsale; Baumel and Witmer, 1993) is essentially absent. At the dorsal edge of the pneumotricipital fossa is a slight ridge, or raised intermuscular scar. A concavity lying just dorsal to this ridge (fig. 2A) may correspond to a feature identified as the m. scapulohumeralis cranialis attachment in *Presbyornis pervetus* (Ericson, 1999) that is also present in the presbyornithid *Telmabates antiquus* holotype (AMNH 3170). In IGM 100/1309, this scar is not bounded dorsally, while in *Presbyornis pervetus* and *Telmabates antiquus* this scar is bounded by a continuation of the dorsal edge (crus dorsale; Baumel and Witmer, 1993) of the pneumotricipital fossa.

A second fossa (fig. 2A) strongly undercuts the posterodistal edge of the humeral head and is open to the capital incisure developed between the head and the well-projected ventral tubercle. Just dorsal to the humeral head, a scar-marked dorsal tubercle is visible (fig. 2A). From the preserved fragment of the deltopectoral crest it cannot be determined whether it was deflected anteriorly or dorsally. The proximoposterior surface of the crest is concave. The lig. acrocoracohumerale attachment is developed as a discrete fossa, rather than as a transverse groove.

IGM 100/1310 is a slightly abraded proximal left tibiotarsus from an avialan approximately the size of *Gallus gallus* (fig. 2B; table 1). Both anterior and lateral cnemial crests are clearly developed. Although the midsection of the patellar crest and antero-

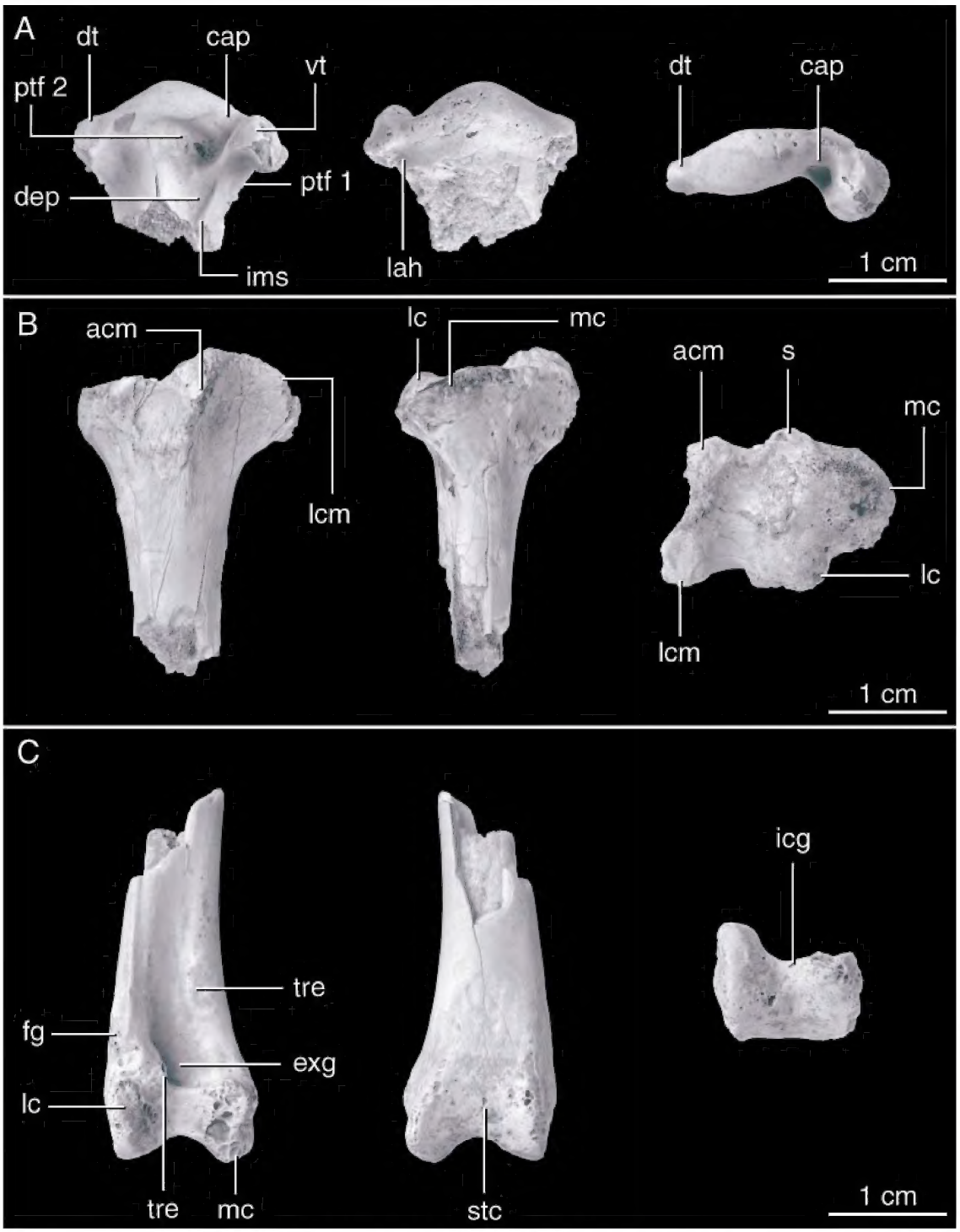

Fig. 2. **A.** IGM 100/1309 in (left) posterior, (middle) anterior, and (right) proximal views. **B.** IGM 100/1310 in (left) anterolateral, (middle) medial, and (right) proximal views. **C.** IGM 100/1311 in (left) anterior, (middle) posterior, and (right) distal views. Anatomical abbreviations: acm, anterior cnemial crest; cap, capital incisure; dep, depression (m. scapulohumeralis cranialis attachment?); dt, dorsal

TABLE 1
Measurements of New Mongolian Fossils (mm)

IGM 100/1309	
Anteroposterior width of humeral head	4.71
Maximum proximodistal height of humeral head	2.92
Dorsoventral maximum length of humeral head	10.47
Width of capital incisure	2.89
IGM 100/1310	
Length of patellar crest	11.66
Maximum width of proximal end of tibiotarsus	16.58
IGM 100/13011	
Width of extensor groove just proximal to condyles	3.52
Maximum mediolateral width of distal end	12.15
Distance of distal end of medial extensor retinaculum scar above proximal surface of medial condyle	7.92
Maximum anteroposterior width of lateral condyle	9.62

proximal portion of the anterior cnemial crest are abraded, it can be determined from their intact portions that neither cnemial crest was well projected proximally. The medial condyle is large and flat, while the lateral is strongly convex. A tuberculated scar (fig. 2B) is projected medially from the midpoint of the medial edge of the tibiotarsus in proximal view.

IGM 100/1311 is a distal right tibiotarsus missing most of its medial condyle (fig. 2C; table 1). The extensor groove is broad and well developed but is not covered distally by an osseous bridge. The extensor retinaculum tubercles are developed, and the fibular groove is deeply impressed and bounded medially by a pronounced ridge (fig. 2C). There is a slight medial deflection and mediolateral widening of the distalmost tibia. The shaft is compressed anteroposteriorly. Posteriorly, the surface for articulation with the tibial cartilage (i.e., trochlea cartilaginis tibialis; Baumel and Witmer, 1993) extends just proximal to the level of the condyles (fig. 2C, center). The medial and lateral edges of this posterior surface are abraded, as is the lateral surface of the lateral condyle.

PHYLOGENETIC ANALYSES

To assess the phylogenetic relationships of the new specimens, they were scored for characters in the Clarke and Norell (2002) matrix, which includes 185 characters informative for the 15 ingroup and two outgroup taxa. This dataset was analyzed using PAUP* 4.0b8[PPC] (Swofford, 2001). The three specimens (IGM 100/1309, IGM 100/1310, and IGM 100/1311) were included as separate terminals since they were unassociated, and there is no evidence that they represent a single taxon. Analysis settings were the same as those in Clarke and Norell (2002): all searches were branch and bound; "amb" in the "Parsimony Settings" menu was selected such that internal branches with a minimum length of 0 were collapsed to form a soft polytomy; and ambiguity was distinguished from polymorphism. The scorings for the new Mongolian specimens are given in appendix 1.

Inclusion of the three terminals IGM 100/1309, IGM 100/1310, and IGM 100/1311 yielded 316 most parsimonious trees (MPTs) 392 steps in length. A strict consensus of these topologies (fig. 3) places the three new elements in a polytomy including *Apsaravis ukhaana* and all taxa more closely related to crown clade Aves than that taxon. Thus, they are all found to be part of Ornithurae (sensu Gauthier and de Queiroz, 2001; see also discussion in Clarke and Norell, 2002 and Clarke et al., 2002). The rest of the recovered topology is the same as that in Clarke and Norell (2002) to the extent that it is resolved.

The Mongolian specimens were then included individually into further phylogenetic analyses. The analysis including only the humerus (IGM 100/1309) of the three specimens produced 2 MPTs also of 392 steps. These two trees differ only in enantiornithine interrelationships. In both trees IGM 100/1309 is placed as the sister taxon of Aves, as part of the clade *Ichthyornis* + Aves.

←

tubercle; exg, extensor groove; fg, fibular groove; icg, intercondylar groove; ims, intermuscular scar; lah, lig. acrocoracohumerale attachment ("transverse groove"); lc, lateral condyle; lcm, lateral cnemial crest; mc, medial condyle; ptf 1, pneumotricipital fossa 1; ptf 2, pneumotricipital fossa 2; s, tuberculated scar; stc, articular surface for tibial cartilage; tre, extensor retinaculum tubercle.

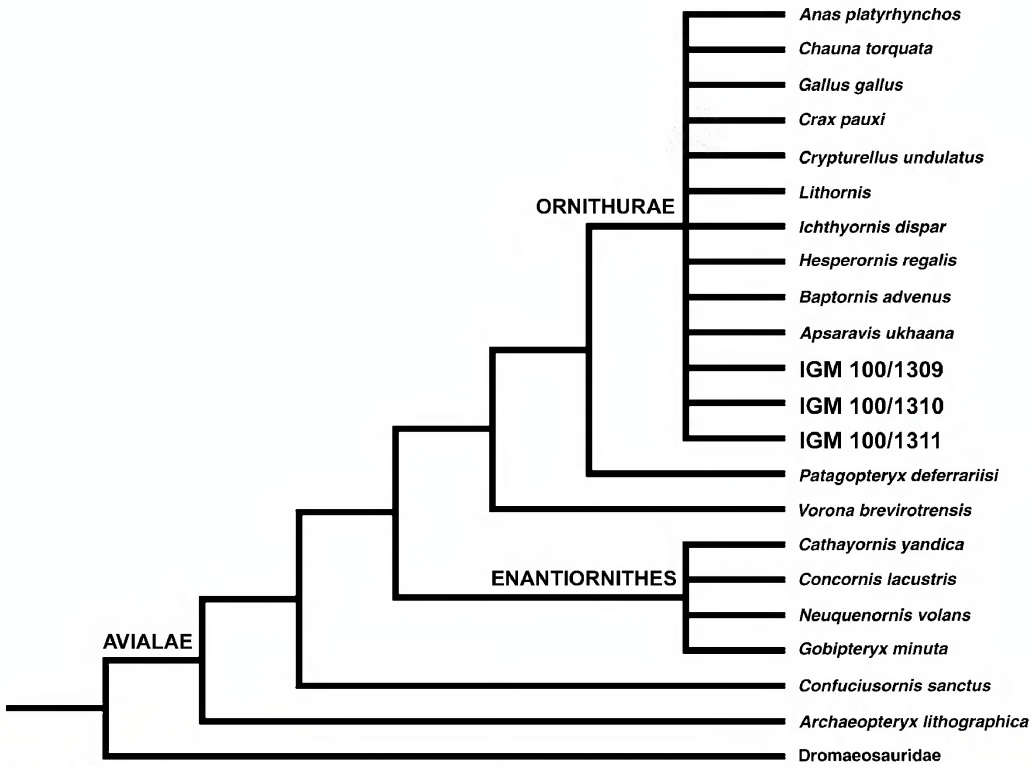

Fig. 3. Cladogram indicating the placement of the three new Mongolian specimens. The strict consensus cladogram of 316 most parsimonious trees (392 steps in length), from analysis of the dataset of Clarke and Norell (2002) scored for the new material (see appendix 1), placed all specimens as part of the clade Ornithurae.

When the proximal tibia (IGM 100/1310; for which only one character could be scored) was included, 28 MPTs resulted (392 steps in length), a strict consensus of which yielded the same topology as the analysis including all three elements. Finally, when only the distal tibiotarsus (IGM 100/1311) was included, 18 MPTs (392 steps in length) resulted. A strict consensus of these trees placed IGM 100/1311 in a polytomy including Hesperornithes plus all taxa more closely related to Aves than *Apsaravis ukhaana*.

DISCUSSION

The proximal humerus (IGM 100/1309) is placed outside crown clade Aves by the lack of a penetrating pneumatic foramen. This foremen, although absent in a variety of taxa nested within Aves (e.g., Ericson, 1997), optimizes as ancestrally present for the crown clade (Clarke and Norell, 2002; Clarke, 2002). Presbyornithid anseriforms and the putative 'transitional shorebird' form family "Graculavidae", which have been reported from the Nemegt Formation (Kurochkin, 2000; Kurochkin et al., 2002), also lack this pneumatic foramen in the humerus. However, there are problems in interpreting this character as indicative of presbyornithid or "graculavid" affinities. As previously mentioned, a pneumatic foramen is ancestrally lacking in Ornithurae (and Avialae; e.g., Clarke, 2002; Clarke and Norell, 2002). On the available evidence, therefore, the lack of a pneumatic foramen could as easily be plesiomorphically retained as apomorphically acquired.

The well-developed fossa excavating the base of the humeral head in IGM 100/1309 is present in a variety of basal avian taxa (e.g., fossil and extant galliforms) as well as in extant Charadriiformes (Baumel and Wit-

mer, 1993), Passeriformes (Bock, 1962), and Procellariformes (Hope, 1999). This fossa has been used simultaneously as evidence to support referral to Presbyornithidae (Ericson, 2000), to the form family "Graculavidae" (e.g., Olson and Parris, 1987; Hope, 1999), to Charadriiformes, and as an example of mosaicism uniting these taxa (e.g., Hope, 1999). As has been repeatedly remarked (e.g., Clarke, 2000; Livezey, 2003), using characters like this fossa (often in small numbers), whose distributions have not been optimized in analysis with appropriate taxon sampling, must result in correspondingly weak systematic hypotheses. More inclusive analyses of basal avian relationships, including further well-represented fossil taxa and, specifically, better preserved exemplars of the taxon known from IGM 100/1309, are necessary to more completely resolve its phylogenetic placement. However, its current, relatively unresolved placement best reflects the most strongly supported phylogenetic hypothesis given the data currently available. The specimen is easily differentiated from both the early Cretaceous *Ambiortus dementjevi* (Kurochkin, 1985) and *Apsaravis ukhaana* (Norell and Clarke, 2001; Clarke and Norell, 2002), the two most complete avialans known from the Mesozoic of Mongolia, by the presence of the distinct fossa excavating the posterodistal humeral head as well as by comparison of nearly every other morphology of the proximal humerus.

Phylogenetic analysis of the proximal tibiotarsus IGM 100/1310 does not resolve whether it is a part of Aves. Relatively low cnemial crests in IGM 100/1310 (even taking into account abrasion) are present, for example, in both *Ichthyornis* and some crown clade lineages (e.g., Tinamidae, Galliformes). These crests are, in contrast, comparatively high in Hesperornithes (Marsh, 1880; Martin and Tate, 1976; Galton and Martin, 2002) and Presbyornithidae (Ericson, 2000) as well as in other crown lineages (e.g., Anatidae, Charadriiformes).

Relative to the other taxa included in the present phylogenetic analyses, it would be ambiguous whether IGM 100/1310 was part of Ornithurae. The only character scorable from the fossil is missing data in *Apsaravis ukhaana*, and the fossil could thus be placed as the sister taxon of the clade *Apsaravis ukhaana* + Aves. This placement would make it potentially outside of a clade known to have a pygostyle homologous with that of Aves (see pygostyle definition, and apomorphy-based definition of "Ornithurae" in Gauthier and de Quieroz, 2001). However, in new analyses (Clarke et al., 2002; in prep.) including two taxa placed as basal to *Apsaravis* (Zhou and Zhang, 2001), a pygostyle is present (Zhou and Zhang, 2001) and two cnemial crests are apparently lacking. Based on these data, IGM 100/1310 is unambiguously part of Ornithurae (sensu Gauthier and de Quieroz, 2001).

The distal tibiotarsus (IGM 100/1311) is placed outside of Aves by the absence of an ossified supratendinal bridge, which optimizes as ancestrally present in Aves (e.g., Clarke and Norell, 2002; Clarke, 2002). Isolated elements identified as part of Hesperornithes from the Nemegt Formation include a distal portion of a tibiotarsus also from Tsagaan Khushu (Kurochkin, 2000; see also Introduction). This specimen was identified as *Baptornis* sp. (Kurochkin, 1988) and later reidentified as "more closely related to *Parahesperornis*" (Kurochkin, 2000: 545). This distal tibiotarsus is nearly identical in morphology to IGM 100/1311. It is also close in size. Its distal mediolateral width is given as 11.7 mm (Kurochkin, 2000), compared to 12.1 mm in IGM 100/1311. Both fossils are from individuals slightly more than one-half the size of *Baptornis advenus* (e.g., AMNH 5101; 19.0 mm), the only named species of *Baptornis* (Marsh, 1880; Martin and Tate, 1976).

These two nearly identical specimens from Tsaagan Khushu also share anteroposterior compression, a broad extensor groove, as well as a prominent fibular groove. These morphologies are present in *Baptornis advenus* (AMNH 5101). The proposed affinities of the tibiotarsus described by Kurochkin (2000) as closer to *Parahesperornis* than to *Baptornis* was supported by "few differences between the lateral and medial condyles, no distal projection of the medial condyle and the remarkable medial position of the extensor groove" (Kurochkin, 2000: 545). These differences from *Baptornis advenus* could not be confirmed. Instead, the extensor

groove on IGM 100/1311 and the specimen commented on by Kurochkin (2000) appear to have an extensor groove slightly more laterally located than in *Baptornis advenus* (AMNH 5101; contra Kurochkin, 2000).

The relevancy of emphasizing comparisons made to Hesperornithes is questionable, however. It depends on how optimistic one is that the morphologies described from the distal tibia will be supported in analysis as synapomorphies of Hesperornithes and/or a subclade thereof. A well-sampled phylogeny with these characters optimized is lacking, and several characters are already known to have a homoplastic distribution (e.g., Martin and Tate, 1976), apparently associated with a diving habitus. For instance, anteroposterior compression of the distal tibiotarsal shaft is seen in a variety of diving crown clade taxa including phalacrocoracids, anhingas, and some sphenisciforms (Simpson, 1946). Further, the compact bone layer in IGM 100/1311 (or IGM 100/1310 for that matter) is not conspicuously thickened in comparison to the condition in *Baptornis advenus* (AMNH 5101) or *Heperornis regalis* (Marsh, 1880).

Tibia IGM 100/1311 from Tsaagan Khushu is similar to *Baptornis advenus*; however, because these similarities are either shared with other diving taxa, have an inadequately investigated distribution, or are plesiomorphic for Ornithurae, referral to this taxon is weak at best. We conclude simply that IGM 100/1311 and the other distal tibia (Kurochkin, 1988, 2000) from Tsaagan Khushu are non-crown clade ornithurines incertae sedis.

Nessov (1992) suggested the presence of a small, possibly flighted, hesperornithine in the Late Cretaceous of Central Asia, and an array of other fragmentary material from across Central Asia has been referred to taxa of Hesperornithes (Nessov and Prizemlin, 1991; Nessov and Yarkov, 1993; Kurochkin, 2000). The referral of this material, and the assumption that all non-crown clade ornithurines with diving modifications are part of a monophyletic Hesperornithes, deserves reappraisal and is, for the reasons stated above, problematic. If, however, future analyses and new discoveries support this conclusion, it would imply that Late Cretaceous ornithurine diversity is low, has been remarkably well sampled, and Hesperornithes are, indeed, a cosmopolitan clade dominating inland riverine and marine environments in the Late Cretaceous of North America and Asia (Nessov, 1992; Kurochkin, 2000).

REAPPRAISAL OF AVIALAN DIVERSITY IN THE NEMEGT FORMATION

Both ornithurine and enantiornithine birds are known from the Nemegt and Djadokhta/Barun Goyot Formations, although ornithurine remains have been more commonly reported from the Nemegt (table 2). After the isolated tarsometatarsus from the Barun Goyot Formation (Kurochkin, 2000) was removed from the Presbyornithidae (Kurochkin et al., 2002) to Avialae incertae sedis, no species or higher taxa less inclusive than Ornithurae and Enantiornithes are known in both the Djadokhta/Barun Goyot Formation and the Nemegt Formation. Previous taxonomic assessment of the Nemegt ornithurines (Kurochkin, 2000) is consistent with Jerzykiewicz and Russell's (1991) conclusion that the fauna from the Nemegt Formation is more similar to North American Late Cretaceous faunas than to Djadokhta/Barun Goyot faunas, as Presbyornithidae, "Graculavidae", and Hesperornithes are taxa which have been proposed to have cosmopolitan distributions and are known from the Late Cretaceous and/or Early Tertiary or North America (e.g., Ericson, 2000; Marsh, 1880; Hope, 2002).

The kind of evidentiary support for the taxonomic assignments of previously described avialan material from the Nemegt varies markedly. The large enantiornithine from Gurilyn Tsav, *Gurilynia nessovi* (Kurochkin, 1999), is known from a proximal humerus and proximal coracoid, and both elements preserve optimized autapomorphies of Enantiornithes (Kurochkin, 2000; i.e., V-shaped humeral head and raised convex surface for scapular articulation on the coracoid [Chiappe, 1996]). However, the referral of partial, isolated cervical and thoracic vertebrae, a tarsometatarsus, and a dentulous mandible to Hesperornithes (Kurochkin, 2000), as well as the distal tibiae discussed here, rests on the more tenuous ground that there

TABLE 2
Comparison of Avialan Remains from the Nemegt and Djadokhta/Barun Goyot Formations

Group	Systematic assignment	Barun Goyot/ Djadokhta formations	Nemegt Formation	Material[a]
Enantiornithes	*Gurilynia nesovi* (Kurochkin, 1999)		X	associated humerus and coracoid
Enantiornithes	Enantiornithes incertae sedis (Elzanowski, 1981; Chiappe et al., 2001)	X (Barun Goyot & Djadokhta)		multiple in ovo embryos
Enantiornithes	*Gobipteryx minuta* (e.g., Elzanowski, 1974, 1977; Chiappe et al., 2001)	X (Barun Goyot & Djadokhta)		3 skulls, 1 partial skeleton
Ornithurae	*Apsaravis ukhaana* (Norell and Clarke, 2001)	X (Djadokhta)		skeleton
Avialae incertae sedis	Presbyornithidae incertae sedis (Kurochkin, 1988, 2000; removed by Kurochkin et al. [2002: 8] to Avialae incertae sedis)	X (Barun Goyot)		tarsometatarsus
Ornithurae	*Judinornis nogontsavensis* (Hesperornithes; Nesov and Borkin, 1983; Nesov, 1986; Kurochkin, 2000)		X	thoracic vertebra
Ornithurae	Hesperornithes incertae sedis (Kurochkin, 2000)		X	tarsometatarsus, cervical vertebra, mandible, tibiotarsus
Ornithurae	**IGM 100/1309, IGM 100/1310, IGM 100/1311 (this paper)**		X	humerus, 2 tibiotarsi
Ornithurae (Aves)	Undescribed remains of "graculavid" charadriiforms, presbyornithid anseriforms, phalacrocoracid procellariiforms (Kurochkin, 2000: 556). Presbyornithidae forelimb described in Kurochkin et al. (2002; *Teviornis gobiensis)*		X	associated distal forelimb, and other unspecified material

[a]Indicated elements are incomplete.

are characters in each of these fragmentary specimens that will, once investigated, optimize as synapomorphies of Hesperornithes or a subclade thereof. We suggest this material be currently considered Ornithurae incertae sedis.

Teviornis gobiensis is the only described Nemegt specimen referred to the avian crown clade (Kurochkin et al., 2002; Presbyornithidae: Anseriformes). Because of this proposed systematic position, *Teviornis* is relevant to the debate concerning fossil evidence for Cretaceous avian divergences (although there appears to have been confusion initially surrounding the holotype specimen's Mesozoic age; Kurochkin et al., 2002: 2). *Teviornis gobiensis* is known from associated, well-preserved wing elements. It was identified as an anseriform based on the "absence of craniocaudal curvature of corpus of carpometacarpus (os metacarpale minus) relative to os metacarpale majus" (Kurochkin et al., 2002: 4), a character from Livezey (1997). However, lack of a bowed metacarpal III is primitive for Avialae (e.g., Clarke and Norell, 2002) and is also plesiomorphically retained within Ornithurae. Not only is this morphology present in nonavian ornithurines (e.g., *Ichthyornis*; Marsh, 1880), a straight metacarpus is present in basal parts of Gal-

liformes (e.g., *Paraortigoides messelensis*, placed as the sister taxon of Galliformes (Mayr, 2000) and Palaeognathae (e.g., *Lithornis*; Houde, 1988), two clades themselves placed as two of the deepest divergences within the avian crown. Therefore, although relative to the set of extant taxa studied by Livezey (1997), the absence of a curved metacarpal III would be a synapomorphy of Anseriformes; with broader taxon sampling (especially of other Mesozoic and early Tertiary taxa), the resultant optimization of this character (as plesiomorphic for Aves) does not provide evidence for the referral of *Teviornis* to Anseriformes.

Teviornis gobiensis was also referred to Presbyornithidae on the basis of three characters from Ericson (2000; Kurochkin et al., 2002), although only one (i.e., the posterodistal extension of the dorsal edge of the carpal trochlea) has been included in any analysis (Ericson, 1997; and is also present in Anhimidae). Another of these suggested presbyornithid autapomorphies, a small interosseus dorsalis canal (Ericson, 2000; Kurochkin et al., 2002), is also present, for example, in Psittaciformes, Charadriiformes (Stegmann, 1978), and, within Anseriformes, in taxa other than the Presbyornithidae (Stidham, personal commun.). The optimization of this character has also not been investigated in any analyses (e.g., Ericson, 1997; Livezey, 1997). In addition, no synapomorphies of Aves, Neognathae or Galloanseres are described for, or appear preserved in, the holotype of *Teviornis gobiensis* to support its proposed position nested within Anseriformes.

In sum, our knowledge of Mongolian Late Cretaceous avialans and the fauna of the Nemegt Formation are augmented by recent descriptive work and the finds described here. However, new and better preserved material will allow a more complete assessment of their phylogenetic and biogeographic implications.

ACKNOWLEDGMENTS

We thank Mick Ellison for photographing the specimens and for preparing figure 2, Evgeny Kurochkin for access to specimens and discussion of Mongolian fossil birds, and Luis Chiappe for helpful comments on the manuscript. Tom Stidham also provided useful information about anseriform morphology and called our attention to aspects of the structure of Hesperornithes long bones. The Frick Fund of the Section of Vertebrate Paleontology, American Museum of Natural History, supported this work.

REFERENCES

Barsbold, R. 1983. Carnivorous dinosaurs of the Cretaceous of Mongolia. Trudy Sovmstnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii 19: 1–120.

Baumel, J.J., and L.M. Witmer. 1993. Osteologia. *In* J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (editors), Handbook of avian anatomy: nomina anatomica avium, 2nd ed. Publications of the Nuttall Ornithological Club 23: 45–132.

Bock, W.J. 1962. The pneumatic fossa of the humerus in the Passeres. Auk 79: 425–443.

Chiappe, L.M. 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*. Münchner Geowissenschaftliche Abhandlungen (A) 30: 203–244.

Chiappe, L.M., M.A. Norell, and J. Clark. 2001. A new skull of *Gobipteryx minuta* (Aves: Enantiornithes) from the Cretaceous of the Gobi Desert. American Museum Novitates 3346: 1–35.

Clarke, J.A. 2000. Setting limits on phylogenetic inference from isolated elements. Vertebrata PalAsiatica 38(suppl.): 9–10.

Clarke, J.A. 2002. The morphology and systematic position of *Ichthyornis* Marsh and the phylogenetic relationships of basal Ornithurae. Ph.D. dissertation, Yale University, New Haven, CT, 532 pp.

Clarke, J.A., and M.A. Norell. 2002. The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. American Museum Novitates 3387: 1–46.

Clarke, J.A., Z. Zhou, and F. Zhang. 2002. An ornithurine from the Early Cretaceous of China. Journal of Vertebrate Paleontology 22: 45A.

Dashzeveg D., M.J. Novacek, M.A. Norell, J.M. Clark, L.M. Chiappe, A. Davidson, M.C. McKenna, L. Dingus, C. Swisher, and A. Perle. 1995. Unusual preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. Nature 374: 446–449.

Efremov, I.A., 1954. Palaeontological research in the Mongolian People's Republic: results of the expeditions of 1946, 1948, and 1949. Trudy Mongol'skoi Komissii AN SSSR 59: 3–32.

Elzanowski, A. 1974. Preliminary note on the palaeognathous birds from the upper Cretaceous of Mongolia. Palaeontologia Polonica 30: 103–109.

Elzanowski, A. 1977. Skulls of *Gobipteryx* (Aves) from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 37: 153–165.

Elzanowski, A. 1981. Embryonic bird skeletons from the Late Cretaceous of Mongolia. Palaeontologia Polonica 42: 147–176.

Ericson, P.G.P. 1997. Systematic relationships of the Paleogene family Presbyornithidae (Aves: Anseriformes). Zoological Journal of the Linnaean Society 121: 429–483.

Ericson, P.G.P. 1999. New material of *Juncitarsus* (Phoenicopteriformes), with a guide for differentiating that genus from the Presbyornithidae (Anseriformes). Smithsonian Contributions to Paleobiology 89: 245–251.

Ericson, P.G.P. 2000. Systematic revision, skeletal anatomy, and paleoecology of the New World early Tertiary Presbyornithidae (Aves: Anseriformes). PaleoBios 20(2): 1–23.

Galton, P.M., and L.D. Martin. 2002. *Enaliornis*, an Early Cretaceous hesperornithiform bird from England, with comments on other Hesperornithiformes. *In* L.M. Chiappe and L. Witmer (editors), Mesozoic birds: above the heads of dinosaurs: 317–338. Berkeley, CA: University of California Press.

Gao, K., and M.A. Norell, 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. Bulletin of the American Museum of Natural History 249: 1–118.

Gauthier, J., and K. de Queiroz. 2001. Feathered dinosaurs, flying dinosaurs, crown dinosaurs and the name "Aves". *In* J. Gauthier and L.F. Gall (editors), New perspectives on the origin and early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom: 7–41. New Haven, CT: Peabody Museum of Natural History Yale University.

Gradzinski, R. 1970. Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert. Palaeontologica Polonica 21: 147–229.

Gradzinski, R., Z. Kielan-Jaworowska, and T. Maryanska. 1977. Upper Cretaceous Djadokhta, Barun Goyot and Nemegt Formations of Mongolia, including remarks on previous subdivisions. Acta Geologica Polonica 27(3): 281–319.

Hope, S. 1999. A new species of *Graculavus* from the Cretaceous of Wyoming (Aves: Charadriiformes). *In* S.L. Olson (editor), Proceedings of 4th International Meeting of the Society of Avian Paleontology and Evolution. Smithsonian Contributions to Paleobiology 88: 231–244.

Hope, S. 2002. The Mesozoic radiation of Neornithes. *In* L.M. Chiappe and L. Witmer (editors), Mesozoic birds: above the heads of dinosaurs: 339–388. Berkeley, CA: University of California Press.

Houde, P.W. 1988. Palaeognathous birds from the early Tertiary of the Northern Hemisphere. Publications of the Nuttall Ornithological Club 22: 1–148.

Jerzykiewicz, T., and D.A. Russell. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. Cretaceous Research 12: 345–377.

Jerzykiewicz, T., P.J. Currie, D.A. Eberth, P.A. Johnston, E.H. Koster, and J.-J. Zheng. 1993. Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. Canadian Journal of Earth Sciences 30: 2180–2195.

Kurochkin, E.N. 1985. A true carinate bird from Lower Cretaceous deposits in Mongolia and other evidence of early Cretaceous birds in Asia. Cretaceous Research 6: 271–278.

Kurochkin, E.N. 1988. [Cretaceous birds of Mongolia and their significance for study of the phylogeny of class Aves.] Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii 34: 33–42.

Kurochkin, E.N. 1999. A new large enantiornithid from the Late Cretaceous of Mongolia (Aves, Enantiornithes). Trudy Zoologicheskogo Instituta RAN 277: 130–141.

Kurochkin, E.N., 2000. Mesozoic birds of Mongolia and the former USSR. *In* M. J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (editors), The age of dinosaurs in Russia and Mongolia: 544–559. Cambridge, MA: Cambridge University Press.

Kurochkin, E.N., G.J. Dyke, and A.A. Karhu. 2002. A new presbyornithid bird (Aves, Anseriformes) from the Late Cretaceous of southern Mongolia. American Museum Novitates 3386: 1–11.

Livezey, B.C. 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis*, and the interordinal relationships of waterfowl. Zoological Journal of the Linnaean Society 121: 361–428.

Livezey, B.C. 2003. Millennial status report as debate wanes [a book review of Mesozoic birds: above the heads of dinosaurs]. Science 299: 1664–1665.

Marsh, O.C. 1880. Odontornithes: a monograph on the extinct toothed birds of North America. United States Geological Exploration of the

40th Parallel. Washington, DC: U.S. Government Printing Office, 201 pp.

Martin, L.D., and J. Tate. 1976. The skeleton of *Baptornis advenus* (Aves: Hesperornithiformes). *In* S.L. Olson (editor), Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. Smithsonian Contributions to Paleobiology 27: 35–66.

Martinson, G.G., A.V. Sochava, and R. Barsbold. 1969. On the stratigraphical division of the Upper Cretaceous deposits of Mongolia. Doklady AN SSSR 189: 1081–1084.

Mayr, G. 2000. A new basal galliform bird from the Middle Eocene of Messel. Senckenbergiania Lethaea 80: 45–57.

Nessov, L. 1986. Pervaya nakhodka pozdnemelovoy ptitsyikhtiornisa v starom svete i nekotoryye drugiye kosti ptits iz mela i paleogena Sredney Axii (The first find of the Late Cretaceous bird, *Ichthyornis*, in the Old World, and some other bird bones from the Cretaceous and Paleogene of Middle Asia). Ekologicheskiye i Faunisticheskiye Issledovniya Ptits (Potapov, Roal'd Leonidovich ed.) Trudy Zoologicheskogo Instituta AN SSSR 147: 31–38.

Nessov, L. 1992. [Flightless birds of meridional Late Cretaceous sea straits of North America, Scandinavia, Russia and Kazakhstan as indicators of features of oceanic circulation.] Byulleten' Moskovskogo Obshchestva Ispytatelet Prirody Otdel Geologicheskii 67: 78–83.

Nessov, L., and L.J. Borkin, 1983. New records of bird bones from Cretaceous of Mongolia and Middle Asia. Trudy Zoologicheskogo Instituta AN SSSR 116: 108–110.

Nessov, L., and B.V. Prizemlin. 1991. [A large advanced flightless marine bird of the order Hesperornithiformes from the Late Cenomanian of the Turgai Strait: the first finding of the group in the U.S.S.R.] Trudy Zoologicheskogo Instituta AN SSSR 239: 85–107.

Nessov, L.A., and A.A. Yarkov. 1993. Hesperornithiforms in Russia. Russian Journal for Ornithology 2(1): 37–54.

Norell, M.A., and J.A. Clarke. 2001. Fossil that fills a critical gap in avian evolution. Nature 409: 181–184.

Norell, M.A., J.M. Clark, and P. Makovicky. 2001. Phylogenetic relationships among coelurosaurian theropods. *In* J. Gauthier and L.F. Gall (editors), New perspectives on the origin and early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom: 49–67. New Haven, CT: Peabody Museum of Natural History Yale University.

Olson, S.L., and D.C. Parris. 1987. The Cretaceous birds of New Jersey. Smithsonian Contributions in Paleobiology 63: 1–22.

Osmólska, H. 1980. Late Cretaceous vertebrate assemblages of the Gobi Desert. Memoires Société de la Geologique de France 139: 145–150.

Perle, A., M.A. Norell, L.M. Chiappe, and J.M. Clark. 1993. A flightless bird from the Late Cretaceous of Mongolia. Nature 362: 623–626.

Simpson, G.G., 1946. Fossil penguins. Bulletin of the American Museum of Natural History 87: 1–99.

Stegmann, B.C. 1978. Relationship of the superorders Alectoromorphae and Charadriomorphae (Aves): a comparative study of the avian hand. Publications of the Nuttall Ornithological Club 17: 1–199.

Swofford, D.L. 2001. PAUP* (Phylogenetic analysis using parsimony [*and other methods] version 4.0b8[PPC]). Sunderland, MA: Sinauer.

Zhou, Z., and F. Zhang, 2001. Two new ornithurine birds from the Early Cretaceous of western Liaoning, China. Chinese Science Bulletin 46: 1258–1264.

APPENDIX 1

Characters scored for the new specimens (IGM 100/1309, IGM 100/1310, IGM 100/1311). Numbers correspond to the characters and the character states listed in appendix 2 of Clarke and Norell (2002; i.e., 106:2 refers to state 2 of character 106 of Clarke and Norell [2002]).

IGM 100/1309 (humerus): 106:1, 107:1, 108:1, 109:0, 110:0, 111:1,112:?, 114:1, 118:0.

IGM 100/1310 (proximal tibiotarsus): (127): 178: 1.

IGM 100/1311 (distal tibiotarsus): 177:2; 180:1, 181:1, 182:1, 183:0, 184:0, 185:2, 186:1, 187:1.